

A Lesser-Known Desert Adaptation:
A Fine-Scale Study of Axis-Splitting Shrubs in the Mojave Desert

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A Lesser-Known Desert Adaptation:
A Fine-Scale Study of Axis-Splitting Shrubs in the Mojave Desert

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Chapter 1

Distribution of axis-splitting species along an environmental gradient

Introduction

Axis splitting: A convergent character among desert shrubs worldwide. All shrubs, by definition, are highly branched from the base. Usually not visible at ground level, shrubs have a short cohesive axis between the proliferating roots and aerial branches. Axis splitting is a phenomenon in which the main axis of a plant segments over the course of development, resulting in physically distinct and functionally independent root-stem-canopy segments. This growth habit has long been noted in shrubs of arid regions worldwide (Diettert, 1938; Moss, 1940; Moss and Gorham, 1953; Ginzburg, 1963; Fahn, 1977; Jones and Lord, 1982), and the axis-splitting habit is so widespread in Asian arid lands that Schenk (1999) calls it a “defining characteristic” of small shrubs of those areas.

Plants achieve this segmentation through several different developmental mechanisms. In some groups (e.g., *Artemisia*), splitting begins through the development of interxylary cork, a layer of suberized tissue which encircles and seals off each year’s new growth (Diettert, 1938; Moss, 1940). Subsequent suberization of the rays functionally isolates segments of the stem from one another (Diettert, 1938). In species such as *Ambrosia dumosa* of the North American deserts (Jones and Lord, 1982; Jones, 1984) and *Zygophyllum dumosum* of the Negev (Ginzburg, 1963; Fahn, 1977), unequal activity of the vascular cambium deforms the stem, and the stem perimeter becomes fluted. The extension of periderm-like tissue into the deepening sinuses seals stem

segments off from one another.

While the mechanisms vary, the end result is the same: the stem's vascular cambium and associated transport conduits become increasingly axially segmented over the life of the plant, inhibiting lateral movement of water, mineral nutrients, and photosynthate. This cambial discontinuity can progress until the plant's main axis physically splits into independently functioning units. In many cases, the segments remain intertwined so that the plant maintains its shrublike growth form, and the split stem is not at all evident until the plant is cut down or excavated (Ginzburg, 1963; Schenk, 1999).

There is no evident phylogenetic relationship linking axis-splitting species, although Schenk (1999) contends that it may be confined to certain families. Prior to this study, axis splitting had been identified in 14 families worldwide, seven of which are present in North America (Schenk, 1999; J. Schenk, unpublished data). The seven North American families are Asteraceae, Fabaceae, Frankeniaceae, Polygonaceae, Rosaceae, Solanaceae, and Zygophyllaceae (Schenk, 1999; J. Schenk, unpublished data). Of these, only Asteraceae and Frankeniaceae have more than one axis-splitting species, and Asteraceae has by far the most, with eight species. This does not necessarily mean that the axis-splitting habit is genetically associated with the Asteraceae, as that family is not only the most speciose in the California desert (± 1300 spp), but is the largest dicot family worldwide (Baldwin et al., 2002).

There is no one functional strategy associated with axis-splitting shrubs. Lowland bajadas of the Sonoran and Mojave Deserts are commonly populated with the vegetative community known as creosote bush scrub (Barbour et al., 1983), which is dominated by

two axis-splitting species, *Ambrosia dumosa* (A. Gray) Payne (Asteraceae) or white bursage, and *Larrea tridentata* (D.C.) Cov. (Zygophyllaceae) or creosote bush (Smith et al., 1997). Throughout this text, these two species will be referenced by their generic names. The axis-splitting morphologies of both *Ambrosia* and *Larrea* have been widely noted (Solbrig, 1977; Jones and Lord, 1982; Barbour et al., 1983; Vasek, 1995), and both species are renowned for tolerating exceptionally low water potentials (Mencuccini and Comstock, 1997; Smith et al., 1997; Pockman and Sperry, 2000). *Ambrosia* and *Larrea* are unrelated, and have very different life histories and morphologies. *Larrea* is large, branched mostly at the base, with resinous evergreen leaves, a “true xerophyte” as defined by Solbrig et al (1977), as it remains photosynthetically active in the driest months and must be extremely conservative in its water use. *Ambrosia* is drought-deciduous, ground-hugging, intricately branched, and brittle. Tolerance of the most extreme drought conditions may be the only characteristic these two species in fact have in common, apart from axis splitting.

That the splitting of the axis arose independently in many different families, and that plants with completely different life strategies have arrived at the same adaptation by different mechanisms, suggests a strong convergence of this characteristic in arid lands. At the same time, there are notable exceptions. Sharing habitat and environmental conditions side by side with axis-splitting species, some desert shrub species (e.g., *Encelia farinosa*) are non-splitters, plants which invariably maintain a stem axis that is round in cross-section and functionally integrated.

Distribution of axis splitting. The presence of non-splitting species in deserts prompted the question of whether axis splitting is, in fact, confined to deserts. A recent

survey of woody shrubs on an aridity gradient of continental scale has shown that axis splitting is indeed widespread in arid regions, and declines in prevalence with increasing precipitation (Goedhart et al., 2004; Schenk et al., in prep.). All shrubs surveyed in mesic climates had stems and vascular cambia that were more or less circular in transection, and were hydraulically integrated (Goedhart et al., 2004). This distribution implies that axis splitting is a morphological adaptation to aridity, but the specific advantages that this behavior confers remain speculative.

The axis-splitting habit is the dominant growth form in some arid regions, but is it an adaptation to low water availability? Knowing that the phenomenon declines in prevalence along a continental-scale aridity gradient, this study sought to discern whether the same pattern would emerge on a fine scale, along a single environmental gradient within an arid ecosystem, the Mojave Desert. The results could increase our understanding of the specific conditions that foster axis splitting, and the habitats in which axis-splitting species are more dominant. To my knowledge, there have been no published studies of axis splitting on a community level.

Hypothesis. In the Mojave Desert, precipitation generally increases with elevation, and plant density, cover, and species diversity increase concomitantly (see Site Description). *Ambrosia* and *Larrea*, both associated with species-poor lowland habitats of extreme aridity, are known to extend into the more diverse upland zone. In this study, the distribution of these two species was predicted to be a model for all axis-splitting shrubs. Axis splitting was expected to be dominant at lower elevation sites; with increasing elevation, plants adapted to the more favorable water regime were expected to outnumber and dominate splitting species. Using the metric of importance value (IV),

which accounts for both abundance and cover (see Methods), I hypothesized that within an arid shrubland, the relative importance of axis-splitting species would decrease in areas that have a greater availability of water.

Site Description

This study was conducted in the eastern Mojave Desert, California. In the rain shadow of the Sierra Nevada, San Bernardino, and San Gabriel mountain ranges, the Mojave has been described as the most arid of all North American deserts (Naumburg et al., 2004). Mean annual precipitation at Mitchell's Cavern is 179.0 mm (Rowlands, 1995). Mitchell's Cavern is the closest and most similar site for which there are data, however it is slightly higher in elevation than the sites used for this study, and the rainfall amount may therefore be an overestimation. Yearly precipitation in the eastern Mojave (east of longitude 117°W) is bimodal, receiving 66% of its annual precipitation during the winter wet season (October-April), and 29% during the summer (Hereford et al., 2006). Monsoonal summer rainfall enters the deserts from the southeast, and the storms lose force as they move to the west and north. Therefore, the eastern Mojave receives some summer rain, but the bimodal pattern is more closely associated with the Sonoran Desert (Hereford et al., 2006, Naumburg et al., 2004; Baldwin et al., 2002). The winter of 2005 brought one season of heavy precipitation in the middle of a multi-year drought (National Climatic Data Center, 2005). Rainfall in that one winter season (October 2004-April 2005) was four times the average rainfall for the same period in 1999-2004 (WRCC - RAWS, 2007). Apart from that one anomalous season, the region has experienced below-average rainfall since 1999, likely an effect of the Pacific Decadal Oscillation (Hereford et al., 2006).

The extent of winter freezing in the Mojave is intermediate between that of the cold Great Basin Desert and the warm Sonoran Desert (Baldwin et al., 2002), with approximately 280 freeze-free days per year expected at Mitchell Caverns (WRCC -

Mitchell Caverns, 2007). As it is generally an upland, the eastern Mojave is a relatively cool desert (Rowlands, 1995). The Mojave Desert region has been considered an extension of the cold Great Basin Desert, but also has been described as the western extent of the Sonoran Desert (Smith et al., 1997). The boundaries between these regions are not distinct, but are instead gradual transition zones (Raven and Axelrod, 1978). Winter temperatures in the Mojave Desert are much more variable than the Great Basin or the Sonoran. Considering temperature variability in combination with precipitation and physiography, Rowlands (1995) concludes that the Mojave is more heterogeneous than the neighboring deserts. The eastern Mojave harbors elements of the cold-desert Great Basin flora as well as warm-desert Sonoran and Mojave species, and may be considered an ecotone, where elements of several desert regions intersect (Smith et al., 1997; Andre, 2006). Its geographic location and varied topography make it a botanically diverse area (Rowlands, 1995); the Mojave Desert has about twice as many native taxa as the Sonoran Desert (Baldwin et al., 2002).

On a smaller scale than the overall regional climatic pattern, precipitation generally increases with elevation. This pattern has been anecdotally noted by many authors (Cody, 1978; Price et al., 2000; Baldwin et al., 2002), but Rowlands (1995) plotted elevational lapse rates of precipitation for several deserts, all of which show a positive correlation between precipitation and elevation, but the eastern Mojave has the highest r^2 . Rowlands' study (1995) found that 68-83% of variation in precipitation is explained by elevation. Many authors have noted the concomitant increase in plant density, cover, and species diversity as elevation increases (Solbrig et al., 1977; McAuliffe, 1988; Padien and Lajtha, 1992, Thompson et al., 2005), and attribute this not

only to the greater precipitation, but also to the lower temperature and potential evapotranspiration at higher elevations (Cody, 1978; Rowlands, 1995).

Emanating from steep mountain ranges, alluvial outwash converges to form vast, gently sloping bajadas (Barbour et al., 1998; Baldwin et al., 2002). Research plots were situated on one such bajada, a south-facing slope that descends from the southern base of the Granite Mountains and terminates in Bristol Lake, a saline dry lake basin. The gradient spans a distance of ca. 40 km and an elevational range of ca. 1000 m.

The bajada elevation gradient served as a proxy for a water-availability gradient. It was not possible to quantify the precipitation variation throughout the sites used for this study; precipitation data is not available on such a fine scale. It is generally accepted that in the Mojave Desert, increasing elevation is accompanied by a parallel increase in precipitation and vegetative cover (Beatley, 1975; Cody, 1978; Thompson et al., 2005). Other researchers (Price et al., 2000) have used a similar bajada slope in the same vicinity as a proxy for a gradient of water availability. Descending the bajada slope, vegetation density and species diversity visibly decline.

Bajada soils are generally mixed gravel alluvium, with some expanses of cobbly desert pavement at the lower elevations. Hundreds of small ephemeral watercourses (washes) and several larger arroyos parallel the slope. Kelbaker Road runs parallel to the slope and provided primary access to the study sites. Several unpaved secondary roads, generally associated with utilities, cross perpendicular to the slope. The bajada is also crossed by a major interstate highway, I-40.

Along Kelbaker Road, five elevation contours (termed “sites”) were subjectively selected to represent a range of elevations along the entire bajada, from just above the

salt flats to the base of the Granite Mountains. Numbered 1 through 5 from lowest elevation to highest, sites 1, 2, and 3 were located south of I-40 on lands managed by the Bureau of Land Management, and sites 4 and 5 were placed north of the interstate, within the Mojave National Preserve (National Park Service). Site locations and elevations are listed in Table 1.

Methods

Field plot sampling design. Three replicate study plots were established at each of the five elevations. Within each plot, three quadrats, 30 m x 4 m in size, were oriented parallel to the evident slope of the bajada. There were, then, 9 quadrats per site. The three quadrats in each plot were spaced 20 meters apart. Plots were well dispersed, at least 500 m apart; their locations were randomly selected within areas of gravelly bajada. Areas crossed by dry washes were excluded from the study, to eliminate the confounding factors of disturbance, substrate compaction, variable moisture availability, and different species composition found in washes (Smith et al., 1997; Barbour et al., 1998). The location of each plot's southwest corner was recorded with GPS (Garmin GPSMap 76S).

All perennial shrubs rooted within a quadrat were recorded by species. Canopy cover for each individual was determined from the greatest horizontal diameter and the diameter perpendicular. Canopy height was measured at the shrub's highest point. All shrub sizes were measured with a folding stick with units in inches only; these measurements were later converted to a metric scale. Canopy volume was calculated using the formula for half ellipsoid, elliptical cone, or cylinder, depending upon the general habit of each species (see Appendix A). From these data, relative density and relative canopy cover were calculated.

Determining what constitutes an individual *Larrea* is often difficult, because of its clonal growth (Vasek, 1995; Smith et al., 1997; Meinzer, 2003), and its tendency to build a mound of aeolian deposited sand around its base (Perkins et al., 2006). Digging between apparent ramets to find below-ground connections proved inconclusive. If two

clusters of stems were >50 cm apart and appeared to arise from separate points, I considered them distinct individuals. Different criteria were applied to clusters of *Yucca schidigera*, which is also clonal (Vasek, 1995), but much more chunky at the base and more tightly clustered than *Larrea*. *Yucca schidigera* clusters were considered separate individuals if separated by >100 cm.

Based on prior work by J. Schenk (Schenk, 1999; Schenk, personal communication) I compiled a list of Mojave Desert species known to be axis-splitting, and a shorter list of known non-splitters. Prior knowledge established the splitting status for 10 of the 26 species found in the study quadrats. As splitting status is rarely visible from the exterior, it requires harvesting the plant to examine the stem cross-section. This determination was performed only on BLM land south of I-40, and for species found only at the upper elevations, harvesting for status determination was performed within the boundaries of the Granite Mountains Desert Research Center. Mature plants were excavated to expose approximately 20 cm of below-ground stem, and the main axis was lopped at 10-15 cm below the first branch. In some cases, this simple test determined splitting status with certainty, e.g., axes of *Psoralea arborescens* and *Krameria grayi* are undisputably circular in cross-section. Some specimens were inconclusive, however, as the difference is not always obvious between a single individual that has split, and the product of two seeds that sprouted from the same spot. A few intractable species required harvesting multiple individuals until a determination was definitive.

Because of the destructive nature of this determination, the status of two species was never resolved. *Lepidium fremontii* was uncommon enough on the bajada that harvesting them seemed inappropriate. *Tetradymia stenolepis* was widespread at site 5,

but all individuals were mature and quite large. There were virtually no young plants to be found. Aware of the risk that harvesting a plant may not provide conclusive determination of splitting status, I could not justify killing a mature plant that may be decades in age. The status of these two species is categorized as “unknown.” Non-woody species (all *Opuntia* spp. and *Y. schidigera*) were presumed to be non-splitting, without investigation.

Many axis splitting shrubs appear fractionally dead. Plants that were completely dead were not included in the study. If a plant had at least one live branch, I considered the entire plant alive and measured its former full extent, assuming that it was that large not too long ago.

Field work was conducted during March and April, 2006. Nomenclature herein follows Baldwin et al. (2002).

Data analysis. Differences in total shrub density, percent cover, and total shrub volume were analyzed in nested design ANOVAs with quadrat nested within plot, and plot nested within site. Importance value (IV) was calculated as the sum of relative cover and relative density for each species. These values were converted to a 0-100 unit scale and were thus considered a percentage of importance (Barbour et al., 1998). Species values were summed by category to compare importance of splitting and non-splitting species, and the relative contributions of woody dicots, succulents, parasitic dicots, monocots, and gymnosperms. Importance of *Ambrosia*, *Larrea*, and splitting species combined were analyzed in nested ANOVAs.

Because importance value and cover are measured as percentages, these data were transformed using arcsine square-root prior to analysis. All of the above analyses were conducted with SAS 9.1 for Windows (SAS, 2002).

Diversity indices, shared species analysis, and rarefaction (species accumulation) curves were calculated using EstimateS 8 (Colwell, 2005). Chao-Jaccard abundance-based estimations of similarity (Chao et al., 2005) for each pair of sites were used to create a similarity matrix, from which a non-metric multidimensional scaling (NMDS) plot was produced, using PRIMER 6 (Clarke and Gorley, 2006).

Results

This study added three new species to the list of known axis splitters: *Menodora spinescens* (Oleaceae), *Thamnosma montana* (Rutaceae), and *Xylorhiza tortifolia* (Asteraceae). Oleaceae and Rutaceae are families new to the list, as well. Four woody shrub species were determined to be non-splitting: *Krameria erecta* (Krameriaceae), *Krameria grayi* (Krameriaceae), *Psorothamnus arborescens* (Fabaceae), and *Salazaria mexicana* (Lamiaceae) (Table 1).

The importance of axis splitting shows an inverse relationship with elevation, as predicted (Table 2, Fig. 1). Axis-splitting species account for 100% of the importance value at site 1, and decline in importance with each increment up the elevation gradient (Table 2, Fig. 1).

The lowest elevation sites are depauperate in every way. Shrub density (number of individuals), species richness, and total shrub cover all increase with elevation (Fig. 2). At site 1, only three species were found in all nine quadrats, and total shrub cover at site 1 is one-fourth the total shrub cover at site 5 (Table 2). Total shrub density increases almost sevenfold between sites 1 and 5, and in fact this measure triples just between sites 1 and 2 (Table 2). Density remains virtually constant between sites 3 and 4, but cover at site 4 is 35% greater than at site 3 (Table 2, Fig. 2). Conversely, between sites 4 and 5, cover remains nearly constant, but density and number of species both increase. The increase is significant only for number of species (Fig. 2). The increases in density, cover, and number of species from site 2 to site 3 are more uniform; all three measures essentially double (Table 2).

Ambrosia and Larrea. *Ambrosia* and *Larrea*, the model axis-splitting species, are the only species that were present in all five sites. Combined, these two species account for no less than 78% of the total importance value at all sites except site 5 (Table 2, Fig. 1). At sites 1 and 2, approximately 97% of the total importance value for all shrubs is explained by these two species (Tables 2-3), but the distribution of both species is extremely patchy at site 1 (Fig. 3). Together, *Ambrosia* and *Larrea* decline in importance with each increase in elevation (Fig 1). Importance values for *Larrea* peak at site 1, decline significantly between sites 1 and 2, and then steadily but less precipitously decline at all succeeding elevations (Fig. 3). Even as axis splitting in general is declining in importance, *Ambrosia*'s IV briefly increases and attains its maximum level at sites 2 and 3 (Fig. 3). While *Ambrosia* declines in IV at site 4, it still maintains great importance in some quadrats (Fig. 3) and is more important than *Larrea* (Table 2). This relationship reverses at site 5, as *Ambrosia* is barely present at all at site 5; *Larrea* is diminished at site 5, but still maintains a greater IV than any other species. At site 1, importance value for *Ambrosia* is the lowest of all sites except site 5 (Fig. 3, Table 3), its cover and density are both low relative to sites 2 through 4 (Table 2), but its importance is relatively large simply because there is hardly anything else there. *Ambrosia*'s IV at site 1 is most similar to that of site 4, but the difference in *Ambrosia*'s cover and density between those two sites is approximately sixfold (Table 2). This is because site 4 contains an abundance of species which appear in substantial numbers (Table 3), so that it takes a lot more *Ambrosia* plants to maintain the same importance value as site 1. The great variability for both species at site 1 (Fig. 3) owes to the overall lack of diversity and

very low density at that site. Most quadrats contained only a few plants, so IV was easily skewed.

Despite its competitive edge due to overall greater size, *Larrea* had greater importance than *Ambrosia* only at sites 1 and 5. At site 5, where *Ambrosia* is nearly nonexistent, *Larrea* has likewise declined in number and its IV is lower there than in any other site. Two of the nine quadrats at site 5 had no *Larrea* or *Ambrosia* at all, and these two quadrats were not in the same plot. Yet at site 5, *Larrea* maintains an IV greater than any other species, because each plant is so large. *Larrea*'s cover at site 5 is almost exactly equal to the total cover of all other splitters combined, yet its IV is relatively low, because it is outnumbered. Only *Yucca schidigera* is competitive with *Larrea* in individual plant volume at site 5 (data not shown).

Breaking IV down into its components (Table 2) shows that *Ambrosia* competes in numbers, *Larrea* in size. A few individuals of *Larrea* can add up to substantial importance. Table 2 demonstrates how importance value dampens the effect of few large individuals by incorporating density. *Ambrosia*, in contrast to *Larrea*, is a small shrub which is nonetheless extremely important because it appears in astronomical densities, particularly at sites 3 and 4 (Table 2). No other species comes close to *Ambrosia*, in numbers, at any site. The second greatest density for any other species at any site is *Coleogyne ramosissima*, with 53 individuals at site 5, followed by *Acamptopappus sphaerocephalus* with 51, also at site 5 (data not shown). The consistent importance of *Ambrosia* at sites 1-4 make its sudden disappearance at site 5 quite striking. The species, which maintained an importance value of >40% at every other site, suddenly became virtually nonexistent with only 7 individuals counted in all 9

quadrats, compared with 237 individuals at site 4 (Table 2). The importance of *Ambrosia* at Site 5 was among the lowest for any species at that site (Table 3). Only *X. tortifolia* and two species of *Opuntia* are less important.

Site differences along the elevation gradient. Rarefaction curves (Fig. 4) indicate differences in species richness among the elevations. The data points in Fig. 4 are not cumulative quadrat values but are Mao Tau species richness estimates, derived from 50 randomizations of the data within each site to estimate total number of species found, as a function of sampling effort (Colwell, 2005). The curves correlate with the means, standard deviations, and ANOVA-reported mean separation results reported in Fig. 2B-C. At site 1, the rarefaction curve (Fig. 4) is compact due to low density; each succeeding curve extends farther on both axes, with each quadrat adding individuals as well as species. Supporting the mean separation letters of Fig. 2B, the Fig. 4 curves show that individual density at site 1 is much less than that of site 2, and sites 3, 4, and 5 are similar.

The compact curves for Sites 1 and 2 demonstrate how very few species and few individuals were found there. Each increase in elevation shows a corresponding increase in density and species richness. Sites 3, 4, and 5 have comparable densities but distinct values for species richness (Fig. 4). The total number of individuals observed at site 3 is 364 plants, which corresponds to 11 species. At comparable values of number of individuals at Sites 4 and 5 (369 and 362.7, respectively), there were 15 species at Site 4, and 18.7 species at Site 5 (Fig. 4). The left end of the x-axis, where points show the number of species associated with the fewest individuals found in each site, also

demonstrates a strong affinity between sites 1 and 2, and between 3 and 4, but site 5 is distinct from the others, starting with a much greater species richness than any other site.

A plot of absolute numbers of species found at the five sites would increase stepwise: 3, 6, 11, 15, and 19 species. But the plot of mean numbers of species that were found in the nine quadrats at each site shows a much slower accumulation of species (Fig. 2C). The difference in means between sites 4 and 5 is greater than would be expected, knowing the total numbers of species found at each site. This is because the maximum number of species found in any one quadrat at sites 3 and 4 is well below the total number of species counted at that site, reflecting a patchy distribution of species at the middle elevations. The mean number of species per quadrat at site 4 is 43% of the total number of species recorded at that site, while at site 5, the mean number of species per quadrat is 60% of the total (data not shown). This contributes to the shape of the rarefaction curves in Fig. 4: the site 5 curve approaches an asymptote, because there was greater species overlap among quadrats. Site 1 also reaches an asymptote, which makes sense as site 1 only had three species, total.

The nonlinear accumulation of species from site to site may be visualized in the distribution of points in the non-metric multidimensional scaling (NMDS) plot (Fig. 5). Points represent the Chao-Jaccard abundance-based estimations of similarity for each pair of sites. The Chao-Jaccard estimator was chosen because it is a probabilistic model which accounts for the effect of unseen shared species (Chao et al., 2005). The points in the NMDS plot are placed in two non-metric dimensions with no values assigned to either axis. The physical distance between points represents the overall similarity between sites in species composition and abundance. The greatest distance between any

two consecutive sites is between sites 4 and 5 (Fig. 5). Although the axes are not associated with values, it is interesting to note that the sites align in elevation order along the x-axis, and in that dimension, sites 1 and 2 are very close to one another, as are sites 3 and 4.

Discussion

Distribution of axis-splitting species. The distribution of axis-splitting species supported the predictions of this study. The combined importance value of all splitting species steadily decreased along the elevation-moisture gradient, as the importance of non-splitters increased. The decline of splitting species was not nearly as pronounced as expected, however. The precipitous decline of *Ambrosia* and *Larrea*, to a combined total of less than 23% of total IV at site 5, is the pattern we expected for all axis-splitting species. It was surprising to find that *Ambrosia* and *Larrea* did not serve as a model for all axis-splitting species. Instead, a different suite of splitting species came in at the higher elevations to replace them. At site 5, the highest and wettest site, axis-splitting species accounted for approximately 75% of relative cover, relative density, and total importance value. Splitting species other than *Ambrosia* and *Larrea* increased incrementally in IV and every one of its components at site 5. These other splitting species, negligibly present at lower sites, comprised the bulk of the importance of axis splitting at site 5. At site 5, splitting remained important even as the community underwent a substantial change in composition.

What are the “other” splitting species? Every one of them is a woody dicot. Non-splitters increased in importance at site 5, but they were mostly succulents, monocots, and the gymnosperm *Ephedra nevadensis*. *Psoralea arborescens* was the only non-splitting woody dicot at site 5. Woody species that are not axis-splitting proved to be the anomaly in these communities, as only five species of this type were found in all sites. Two of these five species, *K. grayi* and *K. erecta*, are known to be root parasites (Wells, 1960; Simpson and Skvarla, 1981; Baldwin et al., 2002), very likely parasitic on

Ambrosia. At sites 2, 3 and 4, where *K. grayi* was the third most important species after *Ambrosia* and *Larrea*, individuals of *K. grayi* and *Ambrosia* were often found completely entwined, with *K. grayi* branches emerging from beneath individual *Ambrosia* plants, or tightly tucked between a pair of *Ambrosia*. The benefits of parasitism that *Krameria* spp. enjoy, extracting water and/or nutrients from the roots of other plants, evidently exempts them from the as yet unknown selective forces that drive the development of so many axis-splitting species among woody desert shrubs. They certainly are more free from water stress than the plants they parasitize. If only woody, nonparasitic dicot shrubs are considered, non-splitting species never make a significant contribution.

It is unfortunate that I was unable to determine splitting status of *Tetradymia stenolepis*, because the IV of that species alone at site 5 (5.63%) would make a substantial contribution to the total importance of either category.

Site 5 is different. Site 5 was distinctive in greater species richness and in the even distribution of species throughout the site. The diversity of species found within each quadrat closely represented the total assemblage at that site, evidenced by the asymptotic rarefaction curve. The mean quadrat species richness at site 5 was significantly greater than site 4, even though with an absolute total of 19 species found, site 5 was not much more species rich than site 4, with 15 species. All other sites, excluding the extremely species-poor site 1, were much slower to accumulate species.

More importantly, site 5 was distinct from all other sites in the dramatic turnover in species composition. Number of species increased consistently from site 1 through site 5, but the increase was not simply additive. Several species that appeared at the lower and middle elevations did not extend to the higher sites, and a few species had

disjunct distributions. Many of the species which appeared at site 5 were completely absent or insignificant at lower sites. Site 5 saw the appearance of many new species, and the discontinuation of many species from the lower sites.

Two genera, *Krameria* and *Ephedra*, followed an almost identical pattern, with one species present at sites 2, 3, and 4, and a sudden and complete species replacement at site 5. For *Ephedra*, this was consistent with expectation, as the elevation range of *E. californica* is described as <900 m by Baldwin et al. (2002). At site 4, where the average plot elevation was 1068 m, *E. californica* was at the upper limit of its range. *E. nevadensis*, which was found at site 5 only, is expected to reach slightly higher elevations, up to 1100 m (Baldwin et al., 2002). In the case of the root-parasitic *Krameria*, the elevation parameters predicted by Baldwin et al. (2002) did not explain the replacement of *K. grayi* with *K. erecta* at site 5, as *K. grayi* is reportedly found at elevations higher than *K. erecta* (Baldwin et al., 2002), and all sites for this study were within the predicted elevation ranges for both species. Substrate characteristics may have been a controlling factor, as site 5 is much closer to the base of the Granite Mountains than all lower sites. An alternate hypothesis is that *K. grayi* is more specifically associated with *Ambrosia* as a host than is its congener, *K. erecta*. *K. grayi* achieved its peak importance values at sites 3 and 4, where *Ambrosia* was declining in importance but at its peak in number of individuals. I have found no support for this speculation of host specificity, but there has been very little study of *Krameria* and its hosts.

Cacti and yucca, which appeared significantly only at site 5, are associated with warm-season rainfall (Rowlands, 1995; Hereford et al., 2006). Succulence is commonly

considered the classic desert morphology, but the majority of desert plant biomass is not succulent (Gibson, 1998). The combined importance value of succulents and monocots at site 5 amounted to only 11.3%.

It is clear that the areas surveyed in this study consist of more than one community. Sites 1, 2, and 3 may be defined as creosote bush scrub (Barbour et al., 1983), or the creosote bush - bursage [*Larrea-Ambrosia*] association (Rowlands, 1995). A vegetation type dominated by *Coleogyne ramosissima* (blackbrush) is expected to displace *Larrea* at elevations above approximately 1000-1200 m (Barbour et al., 1983; Rowlands, 1995). Barbour et al. (1983) describe the blackbrush community as an ecotone between creosote bush scrub and the pinyon-juniper woodland association of higher elevations, sharing half of its flora with each of the communities that form its boundaries. Site 5 can be seen as the lower extent of the blackbrush scrub community, with *C. ramosissima* not yet in its full expression of dominance, and with elements of higher and lower elevation species intermixed. Site 4 was intermediate, with cover and density comparable to higher elevation sites, but species composition which more closely aligns with the lower elevations. Axis splitting was here found to be important in both the creosote bush and blackbrush communities, but splitting occurred in a different set of species in each community, suggesting that there has been convergence of the axis-splitting trait in multiple arid habitats.

The importance of axis-splitting species at site 5 might have been even greater, if not for recent climatic trends. The field work for this study was conducted in a very dry winter-spring season, which followed on the heels of one unusually wet year in the middle of an extended decadal drought (National Climatic Data Center, 2005). The one

wet year, 2004-2005, had provided a reprieve from several consecutive years of below-average rainfall, and plant and animal populations alike responded positively. For some plants, the benefits were ephemeral, as a corresponding population explosion among lagomorphs ended up costing the shrubs dearly, with intense herbivory in the succeeding drought year. Herbivory became evident at site 3, and increased at sites 4 and 5 (unmeasured personal observation). At site 4, *E. californica* and *A. sphaerocephalus* were favored by vertebrate herbivores. At site 5, herbivory was particularly intense on *A. sphaerocephalus*, *M. spinescens*, *Eriogonum fasciculatum*, and *Ericameria cooperi*. Each one of these species is axis-splitting. Many individuals measured were barely resprouting after having been chewed down to a single branch or a nub. Each of these axis-splitting species would have made a greater showing in percent cover, and ultimately in importance value, as some had obviously been much larger until recently.

Neither herbivory nor drought can account for the sudden decline of *Ambrosia* at site 5, because the plants, living or dead, were just not there. Wells (1960) found the same pattern: *Ambrosia* (*Franseria dumosa*) was by far the most common species in terms of density at 3000 feet, with twice as many individuals as the next most dense species, yet at the next elevation interval, 3250 feet, there was no *Ambrosia* to be found. Wells (1960) concluded that the assemblage dominated by *Larrea* and *Ambrosia* was the northernmost extent of the “impoverished Sonoran Desert vegetation,” and that the richer, *Coleogyne*-dominated assemblage of shrubs found at slightly higher elevations constituted a distinctly “Mohavean Shrub zone.” The blackbrush association may be, by Wells’ definition, distinctly Mojavean but it is also dominated by axis-splitting species.

Stand structure changed significantly along the gradient, with overall density, cover, and species richness increasing in correlation with elevation in a pattern which was consistent with reported trends (Solbrig et al., 1977; McAuliffe, 1988; Padien and Lajtha, 1992), and consistent with the expected precipitation increase along an elevation gradient (Cody, 1978; Price et al., 2000; Baldwin et al., 2002; Rowlands, 1995). There is more to water availability than simply rainfall, however. Precipitation effectiveness increases together with elevation because at higher elevations, lower temperatures reduce soil evaporation and thus extend the growing season (Baldwin et al., 2002). More than half of the Mojave Desert's annual precipitation occurs between November and March, when temperatures are low, and overnight freezing is not unusual. Temperatures become most favorable for plant growth just as the wet season comes to a close. Favorable conditions may last only a few weeks before high temperatures become limiting, and evaporation rapidly depletes soil moisture (Naumburg et al., 2004). Many species documented in this study are drought-deciduous, going dormant during the summer (e.g., *Ambrosia*). For these species, the seasonal window for plant growth is very narrow (Naumburg et al., 2004).

Abiotic factors such as soil texture, composition, and drainage patterns influence water availability as well (Schlesinger and Jones, 1984). Desert landscapes are deceptively homogeneous. From a distance, the gravelly bajada substrate appears uniform in composition and texture, with washes and occasional outcrops the only outstanding features. The intent was to avoid washes when establishing quadrats for this study, but all bajada is lightly washed with sheet flow to some extent. The composition of a bajada depends upon the age of deposit, subsequent soil development, and erosion in

washes (McAuliffe, 1994). Subsurface caliche and clay layers, which inhibit plant growth, are not uniformly distributed (McAuliffe, 1994). Soil nutrients are also heterogeneously distributed, and reflect mineral composition of the parent material as well as the effects of other plants, both positive and negative (Bolling and Walker, 2002). Roads also have been shown to influence plant density and cover (Johnson et al., 1975). The overall pattern was as expected, a precipitation gradient causing plant density, species richness, and percent cover to increase with elevation, but vegetation patterns were variable within some sites, and these differences could be attributed to substrate discontinuities. Some combination of abiotic factors were likely responsible for the extreme variability in density at the mid-elevation sites 3 and 4.

Conclusion. Axis splitting declined along the water-availability gradient investigated in the eastern Mojave Desert, yet it remained the most common form at the wettest sites in this study. Splitting was important in both the lowland arid bajadas as well as in the mid-elevation *Coleogyne* (blackbrush) community. The question of the range boundaries for axis-splitting species remains to be answered in future work.

The most drought-tolerant species are all axis-splitting, but this study confirmed that many other desert-adapted woody dicot species that are not quite so extreme in their drought tolerance are axis-splitting as well. The blackbrush community is a more favorable habitat for plants in general, supporting more species at greater densities, but conditions there still support axis splitting in dicot shrubs. The relative immunity to water stress afforded by parasitism evidently exempts parasitic dicot species from the impetus to split.

The selective force that drives the development of so many unrelated axis-splitting species is still uncertain, but distribution patterns point to water relations. Earlier work has shown that on a continental scale, the phenomenon is common in arid lands and decreases to insignificance in mesic areas (Goedhart et al., 2004; Schenk et al., in prep). This study suggests that the same pattern may be found on a finer scale, with the importance of splitting most pronounced in the driest habitats within deserts. It has been hypothesized that axis splitting is an extreme form of hydraulic segmentation, an adaptation in which xylem structure restricts lateral water movement within a plant (Schenk, 1999). Hydraulic segmentation is most adaptive under conditions of water stress, particularly when water is heterogeneously distributed in the soil in small, isolated patches (Schenk, 1999; Schenk et al., in prep). The modularity and redundancy which result from axis splitting prevent water-stressed sectors from compromising the entire plant. Complementarily, an individual root which contacts a small pocket of water supplies a subset of branches rather than the entire canopy, a conservative strategy when water is limited. When plant sectors are hydraulically isolated, embolisms are restricted, and runaway embolism is curtailed.

The functional consequences of axis splitting has not been well studied, apart from the work of C. Jones (1984). In chapter 2, I will examine the relationship between soil water availability and degree of splitting within a single axis-splitting species, *Ambrosia dumosa*.

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Tables

Table 1

Study sites, elevations of the 3 plots within each site, and GPS coordinates of the southwest corner of the center plot in each site.

	Plot elevations (m)	GPS coordinates
Site 1	288, 294, 298	N 34° 33.893' W 115° 38.219'
Site 2	486, 492, 496	N 34° 37.840' W 115° 39.390'
Site 3	774, 784 798	N 34° 41.998' W 115° 41.205'
Site 4	1063, 1066, 1075	N 34° 44.690' W 115° 39.277'
Site 5	1247, 1259, 1264	N 34° 46.507' W 115° 39.418'

Table 2

Importance value and its components (relative cover + relative density), values totaled for each of the 5 sites, sorted by selected species and by splitting status.

	Site	<i>Ambrosia</i>	<i>Larrea</i>	Other splitters	Total Splitters	Non- splitters	Unknown	Total
IV	1	40.29	57.44	2.27	100.00	0	0	100
	2	58.44	38.51	0	96.95	3.05	0	100
	3	55.43	28.76	3.32	87.51	12.05	0.44	100
	4	47.53	30.69	7.70	85.93	11.57	2.50	100
	5	1.16	21.37	52.78	75.31	19.06	5.63	100
Cover (m ²)	1	9.34	42.82	0.70	52.86	0	0	52.86
	2	29.17	43.03	0	72.20	1.73	0	73.93
	3	55.96	70.56	3.31	129.83	17.39	0.90	148.12
	4	61.69	100.56	9.66	171.91	22.45	5.67	200.03
	5	1.25	77.78	77.74	156.47	40.87	12.30	209.64
Relative cover (%)	1	17.67	81.01	1.32	100.00	0	0	100
	2	39.46	58.20	0	96.24	3.76	0	100
	3	37.78	47.64	1.94	87.36	12.36	0.27	100
	4	30.84	50.27	4.83	85.94	11.22	2.83	100
	5	0.60	37.10	36.94	74.64	19.49	5.87	100
Density (total n)	1	39	21	2	62	0	0	62
	2	144	35	0	179	7	0	186
	3	266	36	16	318	45	1	364
	4	237	41	39	317	44	8	369
	5	7	23	280	310	76	22	408
Relative density (%)	1	62.90	33.87	3.23	100.00	0	0	100
	2	77.42	18.82	0	96.24	3.76	0	100
	3	73.08	9.89	4.39	87.36	12.36	0.27	100
	4	64.23	11.11	10.57	85.91	11.92	2.17	100
	5	1.72	5.64	68.63	75.98	18.63	5.39	100

Table 3

Importance value (%) of all perennial shrub and subshrub species. † indicates species whose splitting status was newly determined in this study.

	Site 1	Site 2	Site 3	Site 4	Site 5
12 splitting species					
<i>Acamptopappus sphaerocephalus</i>	0	0	0	3.98	8.26
<i>Ambrosia dumosa</i>	40.29	58.44	55.43	47.53	1.16
<i>Coleogyne ramosissima</i>	0	0	0.51	0	12.59
<i>Ericameria cooperi</i>	0	0	0	0	4.81
<i>Eriogonum fasciculatum</i>	0	0	0	0.15	4.08
<i>Hymenoclea salsola</i>	0	0	0.28	1.70	8.06
<i>Larrea tridentata</i>	57.44	38.51	28.76	30.69	21.37
<i>Lycium andersonii</i>	0	0	0	0.34	0
<i>Menodora spinescens</i> †	0	0	0	0.16	7.82
<i>Senna armata</i>	2.27	0	0.71	0.87	0
<i>Thamnosma montana</i> †	0	0	0	0.15	7.04
<i>Xylorhiza tortifolia</i> †	0	0	1.82	0.35	0.14
Total splitters	100	96.95	87.51	85.92	75.33
12 non-splitting species					
<i>Encelia frutescens</i>	0	0.44	0	0	0
<i>Ephedra californica</i>	0	0.78	4.36	3.65	0
<i>Ephedra nevadensis</i>	0	0	0	0	5.02
<i>Krameria erecta</i> †	0	0	0	0	1.19
<i>Krameria grayi</i> †	0	1.12	5.13	6.91	0
<i>Opuntia acanthocarpa</i>	0	0	0	0	0.27
<i>Opuntia basilaris</i>	0	0	0	0	0.13
<i>Opuntia echinocarpa</i>	0	0	0	0.15	1.03
<i>Opuntia ramosissima</i>	0	0.71	0	0	1.47
<i>Psoralea arborescens</i> †	0	0	1.12	0	1.59
<i>Salazaria mexicana</i> †	0	0	1.44	0.87	0
<i>Yucca schidigera</i>	0	0	0	0	8.36
Total non-splitters	0	3.05	12.05	11.58	19.06
2 species splitting status unknown					
<i>Lepidium fremontii</i>	0	0	0.44	0	0
<i>Tetradymia stenolepis</i>	0	0	0	2.50	5.63
Total unknown	0	0	0.44	2.50	5.63

Table 4

Importance value (%) of shrubs grouped by type, at each site. Totals may not equal 100%, because species whose splitting status is unknown are not included.

Shrub Type	Site 1		Site 2		Site 3		Site 4		Site 5	
	split	non	split	non	split	non	split	non	split	non
Woody dicots	100.0	0	96.95	0.44	87.51	2.56	85.93	0.87	75.31	1.59
Parasitic dicots	0	0	0	1.12	0	5.13	0	6.91	0	1.19
Succulents	0	0	0	0.71	0	0	0	0.15	0	2.90
Monocots	0	0	0	0	0	0	0	0	0	8.36
Gymnosperms	0	0	0	0.78	0	4.36	0	3.65	0	5.02

Figures

Fig. 1 Stacked area graph showing allocation of 100% IV at each of the five sites, between *Ambrosia*, *Larrea*, and all other axis-splitting species combined. White space at top represents IV of all non-splitting species combined.

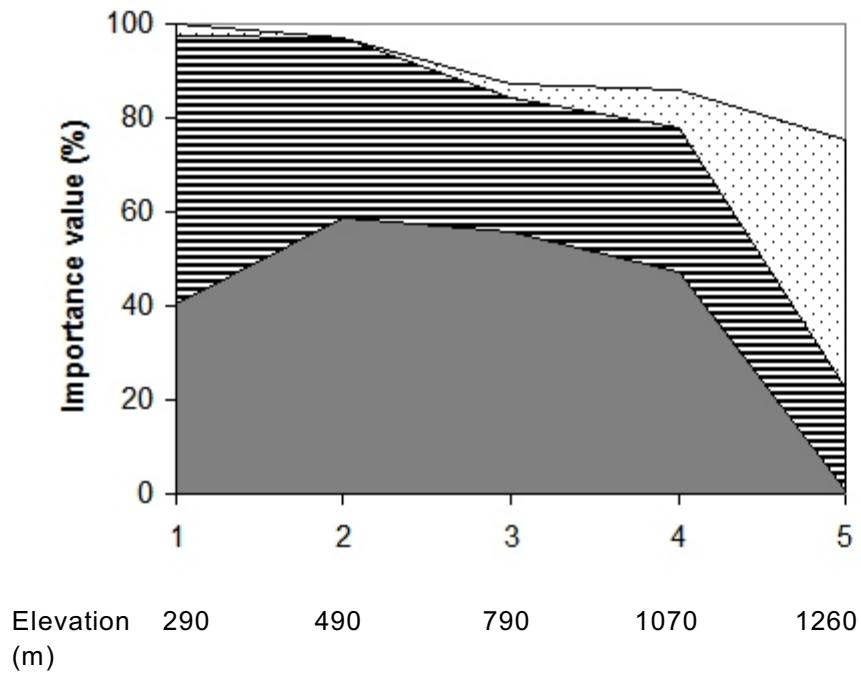


Fig. 2 Overall characterization of sites 1-5, all species combined: percent cover, shrub density, and number of species. Bars represent the mean of nine quadrats at each elevation. Error bars show standard deviation.

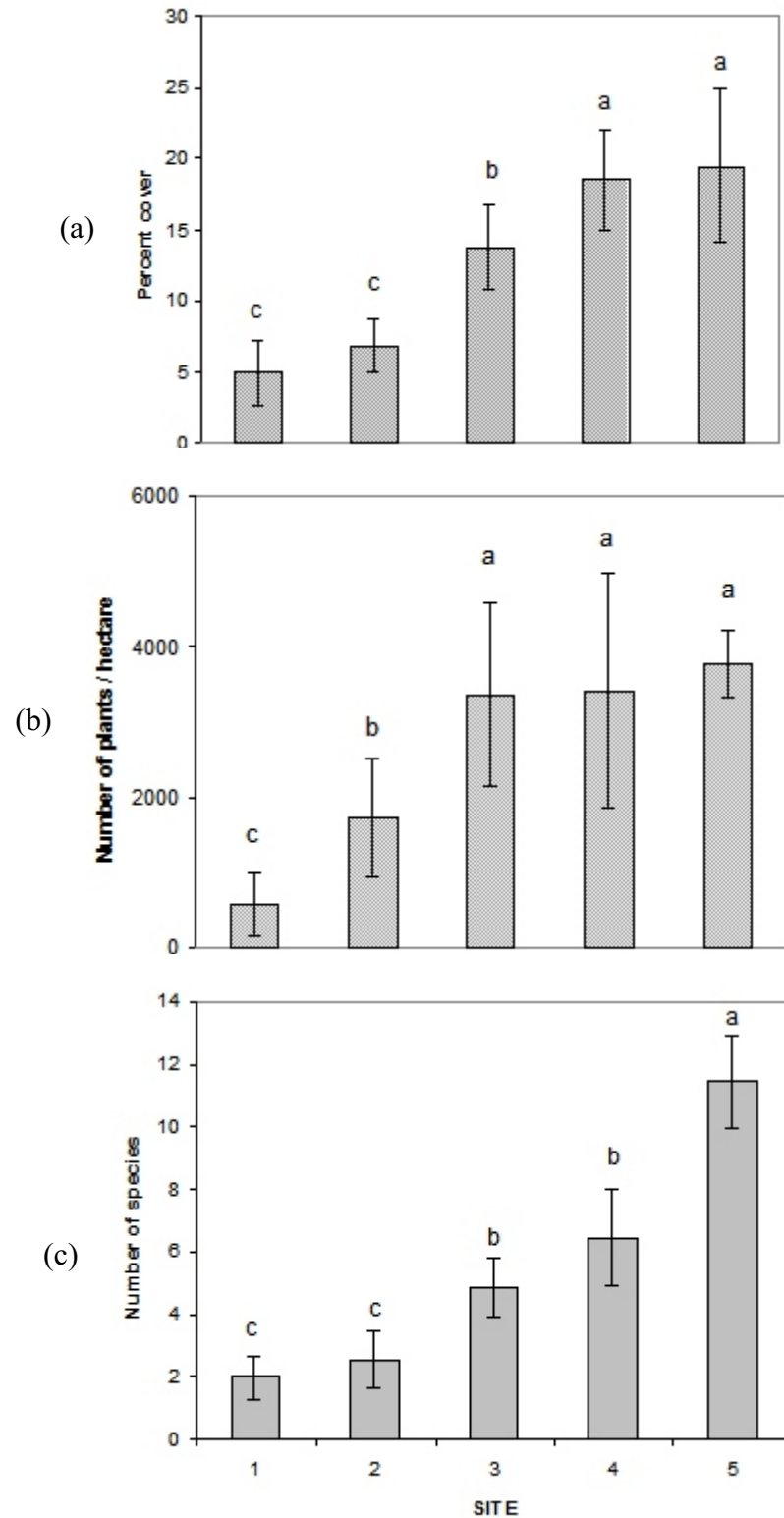


Fig. 3 Box plots of importance values for *Ambrosia* and *Larrea* in nine quadrats at each of the five elevations (sites). Central diamond indicates mean IV for the species.

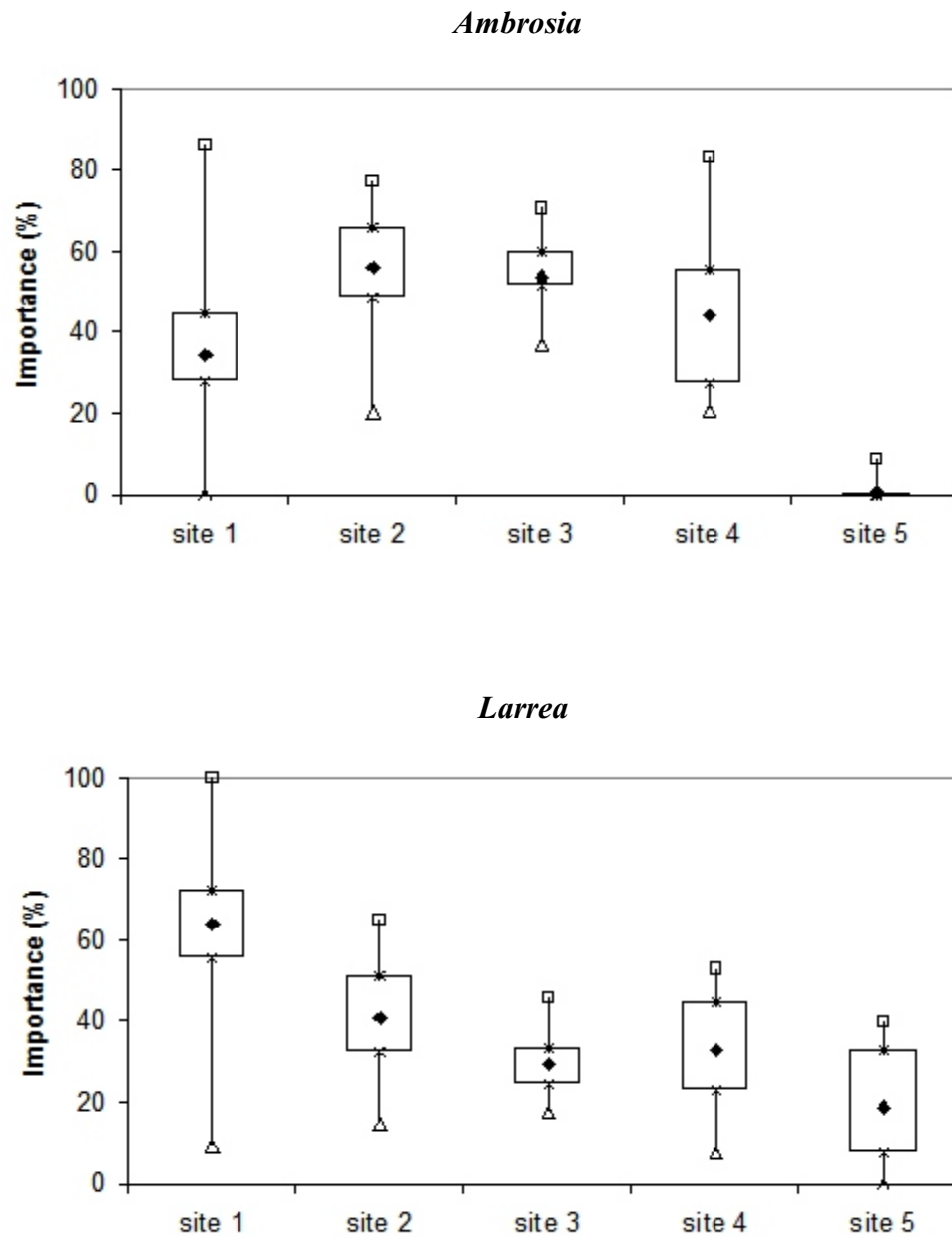


Fig. 4 Rarefaction curves for the five sites, with quadrat as the sampling unit. Data points are Mao Tau species richness estimates, derived from 50 randomizations of the data within each site to estimate total number of species found, as a function of sampling effort.

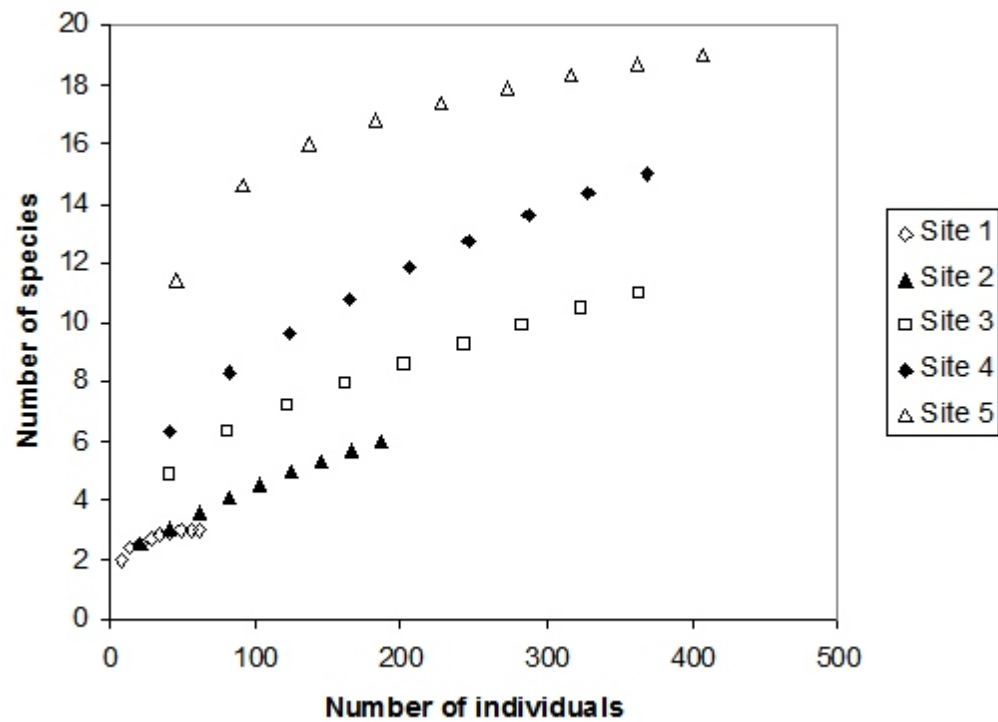
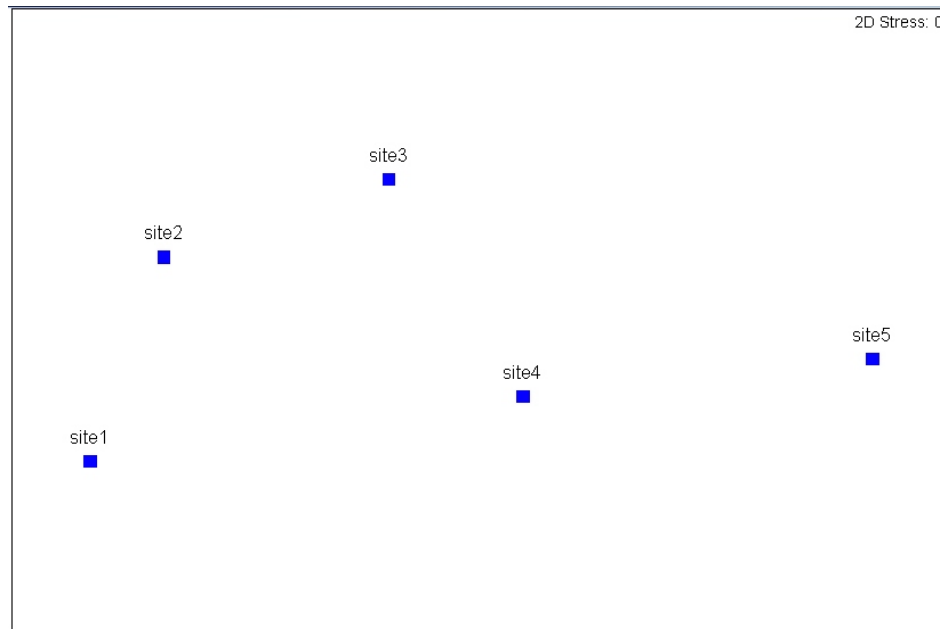


Fig. 5 Non-metric multidimensional scaling (NMDS) ordination plot, in two dimensions. Data points derive from a matrix of Chao-Jaccard abundance-based estimations of similarity between the five sites. Points are placed to minimize “stress,” a dimensionless measure of goodness-of-fit of the regression of fitted and observed distances, on a scale of 0-1. Here, stress of 0 means the ordination is a reliable representation of interrelationships, the points are clearly distinct from one another, and are well-supported.



Chapter 2

Is axis splitting phenotypically plastic within *Ambrosia dumosa*, and is phenotype correlated with water status?

Introduction

In many desert shrubs, the main axis of a plant segments over the course of development, resulting in physically distinct and functionally independent root-stem-canopy modules. This growth habit has long been noted in shrubs of arid regions worldwide (Diettert, 1938; Moss, 1940; Moss and Gorham, 1953; Ginzburg, 1963; Fahn, 1977; Jones and Lord, 1982). The division of the axis has been variously noted over the years as “fission” (Skutch, 1930; Moss and Gorham, 1953), “eccentricity” (Diettert, 1938), or “splitting” (Ginzburg, 1963) of the stem. More recently, the phenomenon has been termed “axis splitting” (Fahn, 1964; Jones, 1984; Schenk, 1999).

Morphological development of the split axis. Axis splitting has been noted in many unrelated plant species and appears to have arisen convergently in several families. Supporting the idea of convergence, shrubs arrive at a dissected axis via several different developmental mechanisms. In some groups (e.g., *Artemisia*) splitting begins through the development of interxylary cork, a layer of suberized tissue which encircles and seals off each year’s new growth (Diettert, 1938; Moss, 1940). Subsequent suberization of the rays functionally isolates segments of the stem from one another (Diettert, 1938). In species such as *Ambrosia dumosa* of the North American deserts (Jones and Lord, 1982; Jones, 1984) and *Zygophyllum dumosum* of the Negev (Ginzburg, 1963; Fahn, 1977), unequal activity of the vascular cambium deforms the stem, and the stem perimeter becomes fluted. The extension of periderm-like tissue into the deepening sinuses seals

stem segments off from one another. There may be other mechanisms as well, but the morphological development of splitting has not been studied in many species.

While the mechanisms vary, the end result is the same: the stem's vascular cambium and associated transport conduits become increasingly axially segmented over the life of the plant, inhibiting lateral movement of water, nutrients and photosynthate. This cambial discontinuity may progress until the plant physically splits into independently functioning units. In many cases, the segments remain intertwined so that the plant maintains its shrublike growth form, and the split stem is not at all evident until the plant is cut down or excavated (Ginzburg, 1963; Schenk, 1999). While the split stem axis has long been documented as a morphological feature of some desert shrubs, it has only recently received renewed attention for its ecological implications.

The ecology of axis splitting. A recent survey of woody shrubs on an aridity gradient of continental scale has shown that axis splitting is indeed widespread in arid regions, and declines in prevalence with increasing precipitation (Goedhart et al., 2004; Schenk et al., in prep.). All shrubs surveyed in mesic climates had stems and vascular cambia that were more or less circular in transection, and were hydraulically integrated (Goedhart et al., 2004). This distribution implies that axis splitting is a morphological adaptation to aridity. The study described in Chapter 1 corroborates this pattern on a fine scale. Splitting species declined in importance value along a water-availability gradient within a desert (Chapter 1). The specific advantages that the axis-splitting behavior confers are still speculative, but may be adaptations to water stress.

Axis splitting as an extreme form of hydraulic segmentation. The vertical ascent of water through the xylem requires a degree of lateral movement as well, as water passes between xylem conducting elements via paired pits on lateral walls (Zimmermann, 1983). In most plants, water moves freely in a lateral direction, and it is common for water and nutrients supplied by a single root to be distributed throughout the canopy (Waisel et al., 1972). When conditions are not optimal, complete hydraulic integration can be a liability, as it can promote runaway embolism, or advance the spread of pathogens. Hydraulic segmentation, where lateral water movement is constrained, is a more conservative strategy. The resulting modularity is most effective when water is limiting (Schenk, 1999; Schenk et al., in prep.), and it is not surprising, then, that segmentation is associated with xeric conditions (Waisel et al., 1972; Orians et al., 2004). Hydraulic segmentation is rare in trees (Zimmermann, 1983; Larson et al., 1994), but widespread among shrubs (Kozlowski and Winget, 1963; Waisel et al., 1972), and shrubs dominate in habitats that are too nutrient-poor or too arid to support trees (Waisel et al., 1972; Barbour et al., 1997). Barbour et al. (1997) make the interesting observation that there are in fact two timberlines in California: one, as expected, at the highest elevations, but also a lower treeline below which only desert scrub can tolerate the heat and aridity.

Most plant species achieve hydraulic sectoriality through anatomical means, without physically splitting (Waisel et al., 1972; Schenk, 1999). Those desert shrubs which do split are thought to express an extreme form of hydraulic segmentation, in which upward movement of water is restricted to one of the splits only (Waisel et al., 1972; Jones and Lord, 1982; Schenk, 1999). Once a stem is fully split, there is no

possibility of water, nutrient, or carbohydrate translocation between sectors. The segments, termed integrated hydraulic units (or IHUs) by Schenk (1999), are completely autonomous.

The modularity and redundancy which result from axis splitting may prevent water-stressed sectors from compromising the water status of the entire plant, by restricting hydraulic failures to a limited sector of the plant (Schenk et al., in prep). Complementarily, an individual root which contacts a small, isolated pocket of water supplies a subset of branches rather than the entire canopy, a conservative strategy when water is limited, and even more effective when water is heterogeneously distributed (Schenk, 1999). In his review of the phenomenon, Schenk (1999) points out that what he terms “clonal fragmentation” does not in itself improve a plant’s ability to forage more widely for resources, as in most axis-splitting species the ramets are as tightly interwoven as they would be if the axis were not split. Axis splitting is thus hypothesized to be a risk-spreading strategy in a water-limited environment, where rainfall is sporadic or seasonal, and the dispersion of soil water may be heterogeneous (Schenk, 1999). The redundancy of multiple independent modules leaves open the option to abscise non-productive segments without compromising the entire genet (Schenk, 1999).

Apart from noting its presence or absence on a regional scale, there has been virtually no functional study of the phenomenon of axis splitting. The work of Jones (1984) is a notable exception, in which water potential of individual branches was found to vary significantly within large individuals of the axis-splitting species, *Ambrosia dumosa*.

Goals of this study. The foregoing discussion of axis splitting as an extreme form of hydraulic segmentation is the most robust explanation for the phenomenon to date. However, it is a hypothesis and is only beginning to be tested. This study attempted to correlate the development and function of axis splitting plants with environmental conditions. Specific goals were twofold: to determine whether there is plasticity in the development of the split axis in response to the availability of water, and to detect axis splitting's functional consequences in terms of within-plant variation in water relations.

It is not known whether the initiation of cambial fluting, the precursor to axis splitting, is triggered at the same developmental stage in all individuals. If this is the case, then plants of the same age should show a comparable degree of cambial deformation. If aridity or the heterogeneous distribution of water in arid soils is a condition that accompanies and possibly drives axis splitting, how then do known axis-splitting species behave when water is more freely available in the soil? Is the onset or rate of cambial irregularity influenced by environmental cues? Variation in the degree of splitting within a species has not been studied. My goal was to establish whether axis splitting is phenotypically plastic by comparing the degree of axial segmentation in young plants of a single species, of comparable age, growing in proximity to one another, but in contrasting habitats. My hypothesis was that within a species and within a size cohort (as a proxy for age), cambial irregularity, the precursor to splitting, would be more advanced in dry sites.

Modules that function independently may each experience different degrees of water stress, and therefore plants that are split might be expected to show variation in

xylem pressure potential among branches within a single plant. A second facet of this study examined whether there was correlation between the degree of fluting and within-canopy variability in water status. My hypothesis here was that within-canopy variation would be greater in plants that were further advanced in cambial fluting.

Ambrosia dumosa (A. Gray) Payne (Asteraceae) was selected as the study species because the developmental trajectory of the split axis is understood in this species (Jones and Lord, 1982), and because it is extremely common on Mojave Desert bajadas. Hereafter, the species shall be identified by its generic name.

Field comparison of contrasting habitats served as a proxy for experimental manipulation. Shrubs growing on undisturbed bajada were compared with individuals of the same species growing on the edge of an unpaved road. Road edges are expected to positively affect water availability, from two causes. First, roads in deserts function like a dam, forcing water to collect on the uphill side (Johnson et al., 1975). Water thus pooled infiltrates more deeply than on unaffected bajada, where rainfall evaporates more readily from upper soil layers (Johnson et al., 1975). Deep water storage means that a greater amount of precipitation water is locally available to plants, and for a longer period (Johnson et al., 1975). In addition, there is a sheeting effect caused by roads. Compacted road material prevents water percolation, and so the water pours off the road edges, concentrating water from the entire road surface area into a narrow band (Johnson et al., 1975). This explains why Johnson et al. (1975) saw positive effects on plant growth on both the upstream and downstream edges of roads, but greater enhancement on the upslope side.

Washes, or ephemeral watercourses, seemed like an obvious choice for habitat comparison as well, because wash soils are expected to be wetter (Rowlands, 1995). But the wash habitat was excluded from this study because wash conditions are extremely variable, and washes experience frequent disturbance (Smith et al., 1997). Most importantly for this study, species composition in washes is quite different (Smith et al., 1997), and *Ambrosia*, the focal species, is not common there. The distinctive species composition and patterns of plant distribution found in washes may demand more water, drying these better-hydrated soils more quickly than in dry sites (Rowlands, 1995). For all these reasons, this study compared only bajada and road edge shrubs.

Methods

Plants were selected at the dry end of the environmental gradient described and studied in chapter 1. Sampling effort was concentrated at site 3, and secondarily at site 1, lowland bajada sites that were extremely arid, and low in plant density and diversity. A difference in water availability between the two habitats would be more pronounced there than at the higher elevation sites.

The Mojave Desert region has experienced a multi-year drought which commenced in 1999. Apart from one anomalous season of heavy precipitation in the winter immediately preceding this study (2004-2005), all plants had experienced seven years of water stress. The winter-spring season of 2005-2006, the season in which this data was collected, had reverted to extreme drought conditions.

For detailed site description and long-term precipitation patterns, see Chapter 1.

Sampling. *Ambrosia* shrubs growing directly on road edges or road berms which also met canopy size criteria (between 8.5 and 19.5 inches in all dimensions, leaning towards the low-to-center part of that size range) were selected. Complementary *Ambrosia* plants which matched size parameters were selected in undisturbed bajada nearby. Aerial branches were removed from the selected shrubs, the plants were excavated to expose approximately 20 cm of underground stem, and the main axis was lopped below ground level, at 10-15 cm below the lowest branch.

A total of 27 plants were harvested. 21 samples were collected at site 3; 12 from bajada and 9 from road edge. 6 samples were collected at site 1; 4 from bajada and 2 from road edge. All samples were collected in April 2006.

Water potential measurements. Prior to the sampling procedure above, a subset of the selected plants in each habitat were first tested for within-canopy variation in xylem pressure potential (ψ). Using a pressure chamber (PMS Instruments, Corvallis, Oregon, USA), ψ was measured on as many as eight major branches per individual shrub. The eight branches were chosen at every 45-degree azimuth clockwise from north, and were numbered to indicate the branches' orientation. These measures were taken on a total of 17 plants. Three bajada plants were measured at site 1. At site 3, ten bajada plants and four road-edge plants were subjected to the pressure chamber prior to harvest.

Of these 17, ten of the plants were measured midday and seven were measured predawn (Appendix B). Some plants show fewer than eight measures (Appendix B) due to mechanical failures and the decision to reject some values which were more than 2 standard deviations from the mean, as it was suspected that those branches were dead or dying.

Pressure chamber measurements were taken during a two-week period, April 6-19, 2006. April is usually the closure of the "wet" season, but the area had received little measurable precipitation in recent months due to the extended drought, noted above. One small storm left 12.7 mm of rain between April 3-5, prior to the beginning of the study. During the two weeks of xylem pressure potential measurement, precipitation was recorded only once, 2.0 mm on April 14. Precipitation data is recorded by the National Park Service at Norris Camp, which at ca. 1200 m is 400-900 m higher in elevation than the sites where the ψ data were collected. It is likely that little to no rain fell at the study

sites. At the sites where ψ data were collected, soils remained visibly dry; soil moisture was not quantified.

Laboratory methods. Stem axes of harvested plants were re-cut cross-sectionally, 1 cm below the lowest branch, using a jeweler's saw. The stem transections were photographed, and the resulting images were used as templates to trace the vascular cambium outline using ArcView GIS 3.2 (ArcView, 1992). To determine dissection index (DI), or degree of segmentation, for each sample, the ArcView software's calculations of perimeter and area for each shape were substituted into the equation

$$DI = p \sqrt{\pi} / \sqrt{A(2\pi)}$$

where p = perimeter, A = area, and $DI = 1$ for a circular area

DI is a dimensionless value. For samples that had split axes and multiple shapes, perimeters and areas were totaled.

Stem cross-sectional area was calculated from two or three measures of stem diameter across the cut section, including the periderm. Two diameter measures were used only for those plants that were most nearly circular in cross-section.

Data Analysis. *Ambrosia* canopy volumes were calculated using the formula for a half ellipsoid (Appendix A). Differences in means among dissection index values and canopy volumes in the two habitats were analyzed using ANOVA, with habitat and site as fixed factors. When differences were significant, means were separated using Tukey's HSD test. The relationship of DI to plant size was analyzed by linear regression of DI against canopy volume and against stem cross-sectional area. The DI-size

relationship between the bajada and road habitats was analyzed with ANCOVA to determine covariance and homogeneity of regression coefficients. Stem cross-sectional area data was log transformed to achieve normality.

The relationship between DI and variation in water status among branches was analyzed by linear regression of DI against the coefficient of variation of within-plant ψ measures. The relationship between within-plant mean ψ and DI was analyzed with linear regression as well. Xylem pressure potential data was collected on as many as eight branches per individual. This resulted in a small sample of individual plants, further partitioned among the four paired categories of habitat and time of data collection (e.g., bajada midday, $n = 7$ plants; road midday, $n = 3$). Because the sample size for each group is small, values for mean ψ per plant were not comparable between habitats. However, the total set of ψ measures for each habitat-time category was combined, irrespective of individual plants. Using data thus pooled, a t-test was performed using only midday measures to compare overall ψ in the two habitats. All statistical analyses were conducted with SAS 9.1 for Windows (SAS, 2002), except for the t-test, which was done with Microsoft Excel.

Results

Plasticity. Dissection index among the *Ambrosia* specimens collected at site 1 was not significantly different from that of samples collected at site 3 (Table 1), and therefore data from the two sites were combined to compare the road edge and bajada habitats generally. *Ambrosia* shrubs growing on the open bajada were significantly more dissected than those on road edges ($P = 0.0013$) (Table 1, Fig. 1). Mean DI among bajada plants was 3.24; mean DI among road edge plants was 1.76 (Fig. 1). Bajada plants' DI ranged from 2.16 - 4.98; road edge plants' DI range was 1.04 - 3.28 (Appendix B). A visual image of these DI values is presented in Fig. 2, where it can be seen that the total conducting area becomes extremely constricted as splitting progresses.

Plants used in this study were intentionally selected within a narrow range of canopy size, but canopy volume was compared between habitats, to confirm that this standard had been met. Canopy volume means in the two habitats are almost identical, 0.0194 m^3 among bajada plants and 0.0196 m^3 among road edge plants ($P = 0.9682$). DI was positively related to canopy volume, but not strongly so (Fig. 3).

Photos of the stem cross sections used to analyze DI (Fig. 2) revealed a surprisingly large range of cross-sectional area at the bases of sampled shrubs, despite the similarity in canopy size. Linear regression of DI modeled against stem cross-sectional area was significant (Fig. 4), and more tightly correlated than the relationship between DI and canopy volume. Habitat differences in the regression of DI vs. stem cross-sectional area were analyzed for homogeneity of slopes; slopes were not different from one another, but the y-intercepts (habitats) were significantly different (Fig. 4). Analysis of covariance, using DI as the dependent variable and habitat and stem cross-sectional area

as covariates, confirmed that DI was significantly larger for a given size stem area in bajada plants (Table 2).

Water potential. Data were first analyzed to determine whether *Ambrosia* shrubs experienced a different degree of overall water stress in the two habitats. Because of sample size, only plants measured at midday were analyzed. At midday, the mean ψ among all branches of all bajada plants combined (-4.77 MPa) was more negative than that of their compatriots growing on the road edge (-4.16 MPa) (Fig. 5). The difference in overall water status between the two habitats was highly significant ($P = 0.0006$).

Within each plant, between five and eight measures of ψ were taken to determine whether within-plant variation was greater in plants that were more dissected. Coefficient of variation (CV) was used to represent variation in ψ among branches within a plant. There was no relationship between DI and an individual plants' CV in ψ ($P = 0.9322$) (Fig. 6), nor between DI and mean plant ψ ($P = 0.8685$) (Fig. 7). Due to the small sample size, both within-plant CV and within-plant mean ψ were not analyzed for habitat differences. This second analysis of mean plant ψ may be less meaningful because the mean ψ of plants measured at different times of day are not comparable, yet the data are included here for visual comparison. Total raw data is shown in Appendix C.

Discussion

Plasticity. Axis-splitting species are the dominant shrubs in arid lands worldwide. Despite the prevalence of the phenomenon, this is the first field study to examine whether the split axis is influenced by environmental cues. I hypothesized that within a species and within an age cohort defined by plant size, DI would be greater among shrubs growing on the undisturbed bajada than among those growing on road edges. Stem axes of *Ambrosia* plants growing on road edges were significantly less dissected than stems of similar-sized shrubs of the same species growing nearby on the bajada. These results are robust despite small sample sizes, and despite unexpected differences in stem diameters.

The plants were comparable in above-ground size; canopy volume in the two habitats was virtually identical. It is not surprising that compared to stem cross-sectional area, volume is less closely related to DI, because plants were specifically chosen within a narrow canopy size range, so the differences in actual volume are small. However, smaller stem diameters among road edge plants suggest that they may have been younger. Jones and Lord (1982) showed that axis splitting in *Ambrosia* develops progressively over time. It is difficult to determine plant age in desert shrubs by counting growth rings, particularly after seven years of drought. There is controversy over whether growth rings are meaningful or even detectable in desert shrubs. Smith et al. (1997) asserted that desert shrubs do not produce reliable growth rings; McAuliffe (1988) assumed that *Ambrosia*'s growth rings are annual increments. Annual growth rings may be evident only in plants that are very small.

Nevertheless, regression of DI against stem cross-sectional area found that the slopes for the two habitats are the same, with different intercepts. Covariate analysis, which corrects the means to account for differences in the covariate (Sokal and Rohlf, 1995), confirms that when plants of the same stem cross-sectional area are compared, there is a difference in DI between the two habitats. Thus even for a common stem size (and possibly age) road plants were less dissected than bajada plants.

It is unknown whether this difference in DI between habitats results from road edge plants experiencing more favorable conditions, such as greater water availability, but two indirect observations support this hypothesis. The first is that for a given stem diameter, canopy sizes were larger in roadside plants. Secondly, despite the short-term nature of water potential measures, average midday ψ measured over a three week period in April 2006 was also less negative in road edge plants. More direct evidence in support of this hypothesis is needed, e.g., measurements of growth rates, photosynthetic rates, nutrient content of leaves, etc.

Variation in xylem pressure potential. To test whether the advance of axis splitting increases functional isolation of segments, I predicted that there would be greater variation in ψ among individual branches within the canopy of plants that were more dissected. This proved not to be the case. There was no relationship between DI and within-plant CV in ψ . Plants that were fully segmented showed no more ψ variation among branches than those with cambial outlines that were barely fluted. A high degree of variation in water status among branches, even in plants with a very low DI, suggests that *Ambrosia* plants are already hydraulically segmented well before the physical split.

Bajada plants' overall water status was more variable within each time category, as evidenced by error bars in Fig. 5. Plants growing on road edges appear to be less subject to variability in water status, both over the course of a day (size of bars), and within and among individuals (error bars). Predawn measures in both habitats were less negative than those taken at midday, which conforms to well-documented expectations of overall diurnal water status.

Some measures were excluded from the analysis because they appeared to be due to measurement error. It is possible that some of the rejected values reflected embolized branches, in which case these data present a very conservative picture of the full range of water status among these shrubs.

Conclusion. This study found that there was indeed some measure of plasticity in the rate of splitting in *Ambrosia dumosa*. Road edge plants were less fluted than bajada plants, and were evidently able to maintain a relatively large canopy at a smaller stem diameter. The habitat difference can be interpreted two ways. If, according to the findings of Johnson et al. (1975), road edge plants have access to a more plentiful and longer-lasting water supply which limits water stress and extends the growing season, *Ambrosia* shrubs may delay cambial irregularity when soil hydration is favorable for growth. It is also possible that the water supply at road edges is more homogeneously distributed, spatially. This could be a result of the damming effect of roads (Johnson et al., 1975), or possibly because the soils pushed by a grader to the road berm are more well mixed and more uniform in size. That would suggest that it is not simply drought, but heterogeneous water access, that drives axis splitting in *Ambrosia*. The greater

variability in dissection index among bajada plants may be a reflection of soil heterogeneity.

Splitting may enhance a plants' survival at the expense of growth. With smaller stem diameter, the less dissected road plants maintained the same canopy volume as bajada plants. Regardless of whether road plants were younger, this relationship hints that the advance of splitting may limit a plant's canopy size, inhibiting its ability to capitalize on favorable conditions. North and Nobel (2000), in a study of *Agave* root proliferation in heterogeneous microsites, concluded that for slow-growing desert perennials, developmental plasticity along existing individual roots (in the form of delayed suberization in regions where water was more available), may be less costly than the proliferation of new lateral roots in favorable microsites. Certainly *Ambrosia* is not *Agave*, but there could be a corollary in terms of conservative response to favorable conditions among desert plants. Both strategies minimize risky investment in an uncertain environment, and instead concentrate efforts on structures that are already in place.

Ambrosia plants may be hydraulically segmented well before the physical split, or even before the onset of cambial fluting. The advantages of proceeding from modularity to a completely split axis remain obscure. The loss of structural integrity can only be a biomechanical liability. Perhaps a complete break is the only way to ensure functional independence of segments, so that water is not shared among modules, and the spread of embolisms is restricted. The functional advantages of axis splitting are unresolved, but the overwhelming prevalence of the phenomenon in woody desert shrubs speaks to its importance as a growth strategy and demands further study.

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Tables

Table 1

Dissection index of 27 *Ambrosia* specimens at two sites (sites 1 and 3) and two habitats (bajada and road edge). Sites are not different from one another. DI is significantly affected by habitat.

Dependent variable	Dissection index			
Source	Sum of squares	d.f.	<i>F</i> -value	<i>P</i>
Site	0.268	1	0.43	0.5196
Habitat	8.400	1	13.39	0.0013
Site × habitat	0.105	1	0.17	0.6859

Table 2

Analysis of covariance showing relationships of dissection index to habitat, with log-transformed basal stem size as the covariate.

Dependent variable	Dissection index			
Source	Sum of squares	d.f.	<i>F</i> -value	<i>P</i>
Log cross-sectional area	22.465	1	96.16	<0.0001
Habitat	1.084	1	4.64	0.0420
Log x-s area × habitat	0.313	1	1.34	0.2587

Figures

Fig. 1 Dissection index of 27 *Ambrosia* shrubs sampled in two different habitats, road edge and bajada. Habitat means (Road = 1.7583; Bajada = 3.2390) are significantly different ($P = 0.0013$). Error bars represent standard deviation.

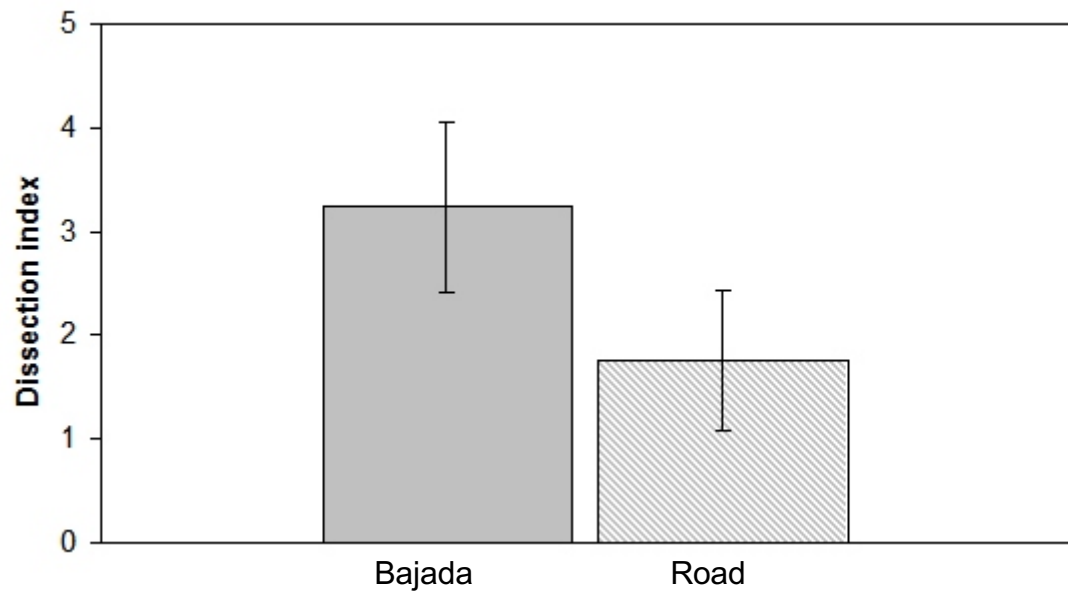


Fig. 2 A sample of photographs of stem cross-sections, plant i.d. numbers, and DI values. Minor scale increments are millimeters. Cambial outlines were traced from these images to calculate DI.

ROAD EDGE



3-07 DI 1.136



3-33 DI 1.824



3-35 DI 3.283

BAJADA



3-10 DI 2.250



3-17 DI 2.598



3-24 DI 4.975

Fig. 3 Relationship between stem dissection index and canopy volume of *Ambrosia dumosa* shrubs collected on bajada and road edge, where plants were selected within a narrow range of canopy size. Two of the 27 plants are excluded here because canopy volume was not measured for those individuals. The relationship between DI and canopy volume is significant ($P = 0.0506$).

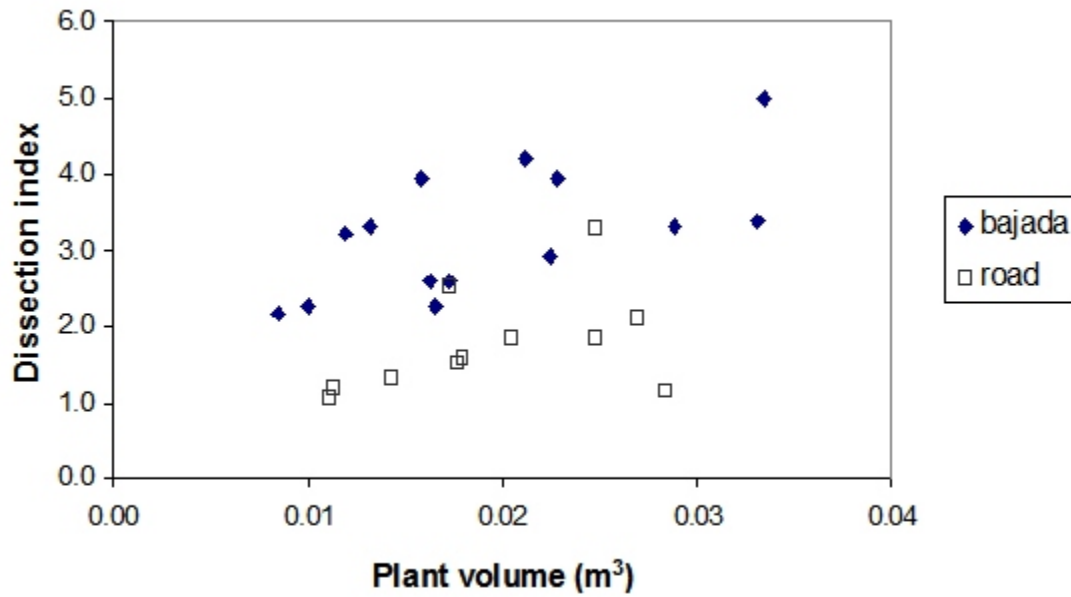


Fig. 4 Relationship between dissection index and stem cross-sectional area ($P < 0.0001$; $r^2 = 0.7431$). The slopes for the two habitats are not different ($P = 0.2587$), but y-intercepts do differ ($P = 0.0420$). Although many bajada plants are larger in cross-sectional area than road edge plants, analysis of covariance determined that when two plants of the same cross-sectional area are compared, there is a significant difference in DI between habitats.

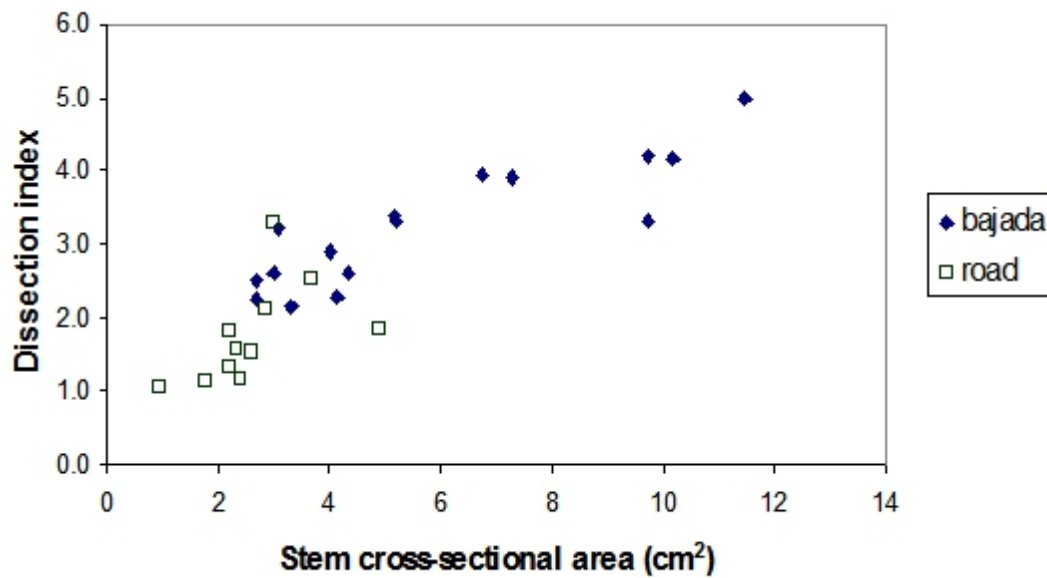


Fig. 5 Xylem pressure potential data, all measures grouped by time of measurement, and by habitat, irrespective of individual plants. Error bars depict standard deviation.

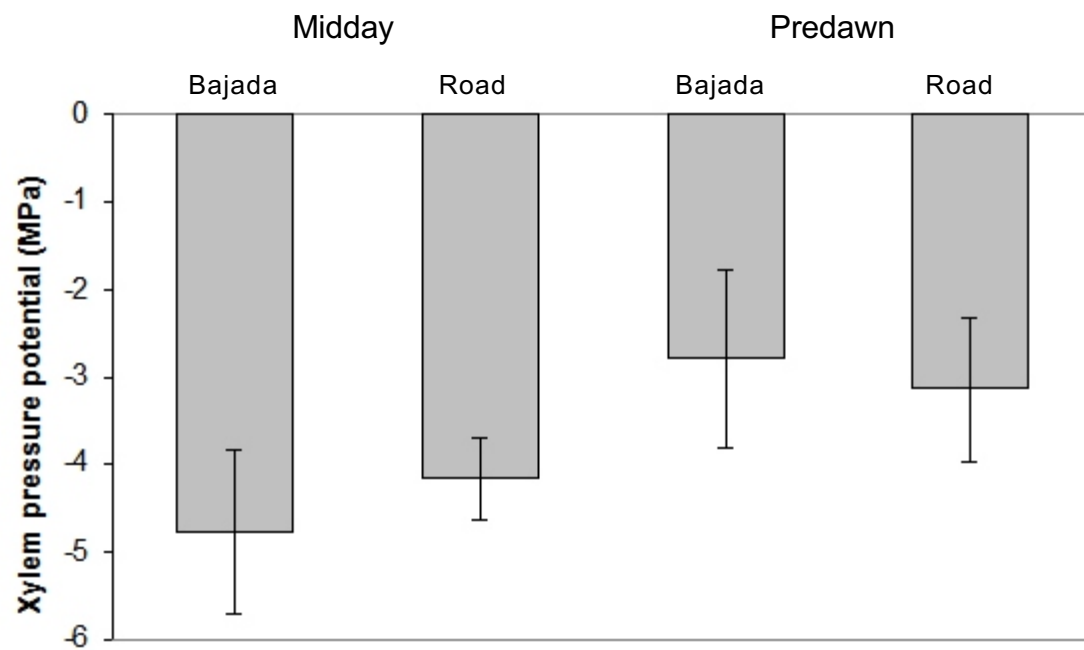


Fig. 6 Linear regression of dissection index (DI) and the variation in xylem pressure potential (ψ) measures within the canopy of individual plants, expressed as coefficient of variation (CV). Coefficient of variation represents variation among 5- 8 ψ measures taken within an individual plant. The relationship between a plant's DI and the CV of ψ is not significant ($P = 0.9322$).

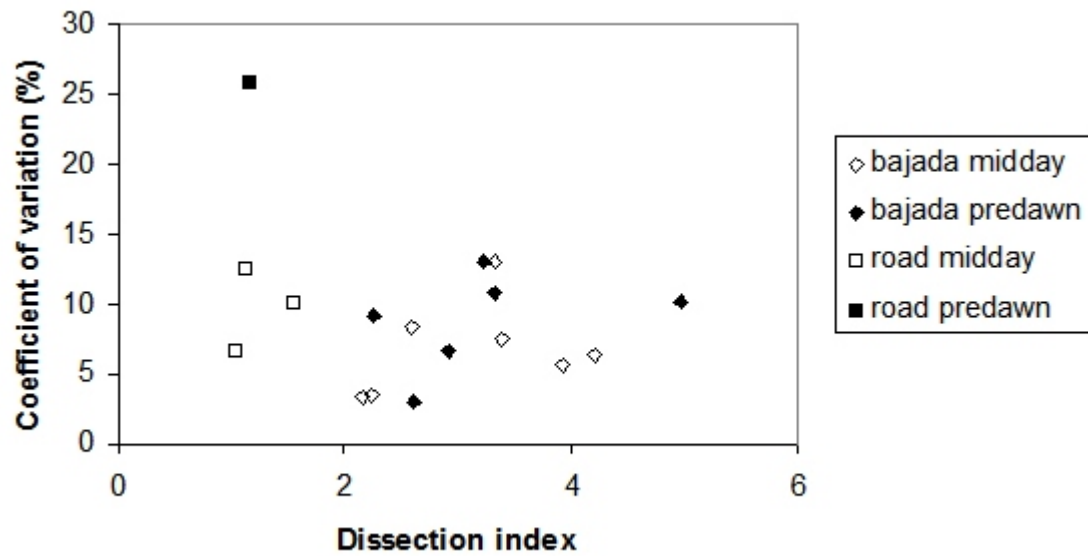
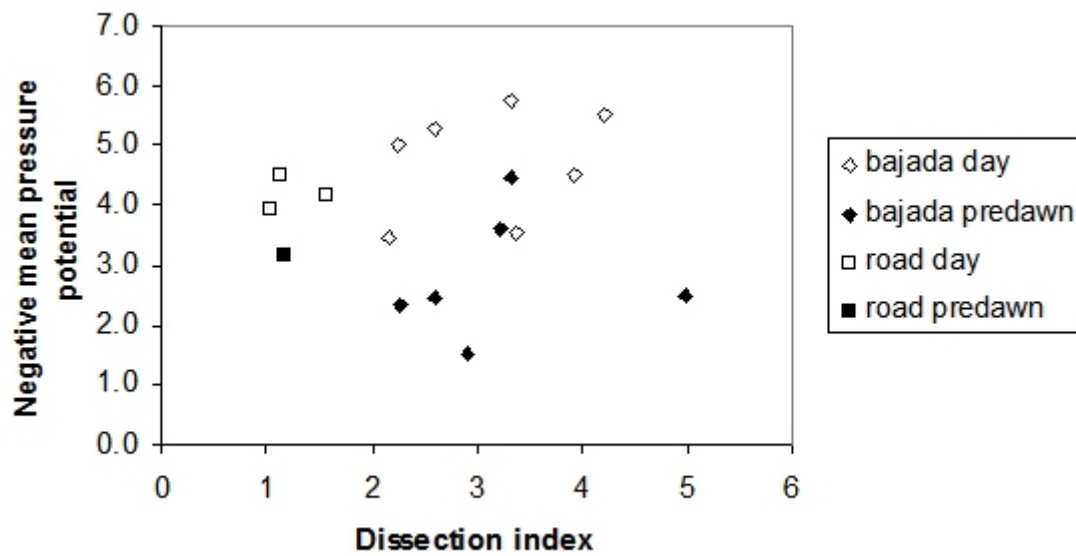


Fig 7 Relationship between dissection index (DI) and negative mean xylem pressure potential (ψ) among all individuals. Xylem pressure is negative, and the ψ values are here expressed as their opposites, for the purpose of visual representation. Data points represent the 17 individuals included in this part of the study, distinguished by habitat and time of ψ measurement. The overall relationship between DI and mean ψ was insignificant ($P = 0.8685$).



Appendix A

Formulas used for calculating volume of shrub species:

Half ellipsoid: $\text{volume} = \pi * ab * h / 6$, where a = greatest horizontal diameter, b = secondary horizontal diameter, and h = height.

Elliptical cone: $\text{volume} = \pi * ab * h / 12$, where a = greatest horizontal diameter, b = secondary horizontal diameter, and h = height.

Cylinder: $\text{volume} = \pi * ab * h / 4$, where a = greatest horizontal diameter, b = secondary horizontal diameter, and h = height.

Species	Volume formula
<i>Acamptopappus sphaerocephalus</i>	Half ellipsoid
<i>Ambrosia dumosa</i>	Half ellipsoid
<i>Coleogyne ramosissima</i>	Half ellipsoid
<i>Encelia frutescens</i>	Elliptical cone
<i>Ephedra californica</i>	Elliptical cone if < 0.055 m in 2 dimensions; half ellipsoid if larger
<i>Ephedra nevadensis</i>	Elliptical cone if < 0.055 m in 2 dimensions; half ellipsoid if larger
<i>Ericameria cooperi</i>	Half ellipsoid
<i>Eriogonum fasciculatum</i>	Half ellipsoid
<i>Hymenoclea salsola</i>	Half ellipsoid
<i>Krameria erecta</i>	Half ellipsoid
<i>Krameria grayi</i>	Half ellipsoid
<i>Larrea tridentata</i>	Elliptical cone
<i>Lepidium fremontii</i>	Half ellipsoid
<i>Lycium andersonii</i>	Half ellipsoid
<i>Menodora spinescens</i>	Half ellipsoid
<i>Opuntia acanthocarpa</i>	Elliptical cone
<i>Opuntia basilaris</i>	Half ellipsoid
<i>Opuntia echinocarpa</i>	Elliptical cone
<i>Opuntia ramosissima</i>	Elliptical cone
<i>Psoralea arborescens</i>	Half ellipsoid
<i>Salazaria mexicana</i>	Half ellipsoid
<i>Senna armata</i>	Elliptical cone
<i>Tetradymia stenolepis</i>	Elliptical cone
<i>Thamnosma montana</i>	Half ellipsoid
<i>Xylorhiza tortifolia</i>	Elliptical cone
<i>Yucca schidigera</i>	Cylinder

Appendix B

Dissection index and stem cross-sectional area for all 27 plants, grouped by habitat and ordered by dissection index. The first digit of plant i.d. numbers identify the collection site number, either site 1 or site 3.

Bajada			Road Edge		
Plant i.d.	Dissection index	Cross-sectional area (cm ²)	Plant i.d.	Dissection index	Cross-sectional area (cm ²)
3-03	2.164	3.301	3-11	1.039	0.950
3-10	2.250	2.688	3-07	1.136	1.767
1-06	2.268	4.155	3-13	1.168	2.405
3-36	2.523	2.688	3-04	1.328	2.204
3-17	2.598	4.337	1-22	1.519	2.616
1-08	2.602	2.986	3-18	1.569	2.337
1-07	2.915	4.035	3-33	1.824	2.204
3-12	3.229	3.064	1-21	1.843	4.909
3-16	3.326	5.208	3-19	2.105	2.835
3-15	3.327	9.759	3-34	2.527	3.687
3-08	3.385	5.174	3-35	3.283	2.986
3-02	3.923	7.306			
1-09	3.943	6.758			
3-27	4.184	10.179			
3-14	4.212	9.759			
3-24	4.975	11.491			

Appendix C

Within-canopy variation in xylem pressure potential. As many as 8 measures were taken around the canopy of an individual shrub. Values for ψ are negative, as they measure negative pressure within the xylem, but they are here shown as absolute values. Mean ψ and coefficient of variation (CV) for each plant, as well as plant dissection index (DI) are included.

Within-canopy negative xylem pressure potential													
Plant	DI	Habitat	Time of measure	1	2	3	4	5	6	7	8	mean	CV
3-03	2.164	bajada	midday	3.5	3.5	3.3	3.3	3.5	3.4	3.6		3.44	3.29
3-10	2.250	bajada	midday	5.1	4.8	4.9	5.1	5.1	5.3	4.8	4.9	5.00	3.55
3-17	2.598	bajada	midday	5.5	5.0	4.6	5.7	5.2	5.9	5.2		5.30	8.30
3-15	3.327	bajada	midday	6.0	4.2	6.0	6.0	6.5	6.5	5.3	5.6	5.76	13.02
3-08	3.385	bajada	midday	4.0	3.5	3.5	3.5	3.1	3.5	3.6		3.53	7.45
3-02	3.923	bajada	midday	4.7	4.5	4.5	4.0	4.8	4.5	4.6		4.51	5.64
3-14	4.212	bajada	midday	5.8	5.5	6.1	5.0	5.5	5.2	5.4	5.7	5.53	6.25
1-06	2.268	bajada	predawn	2.4	2.2	2.3	2.2	2.8	2.1	2.3	2.3	2.33	9.12
1-08	2.602	bajada	predawn	2.5	2.5	2.4	2.5	2.5	2.3	2.5	2.5	2.46	3.02
1-07	2.915	bajada	predawn	1.4	1.4	1.5	1.5	1.5	1.7	1.5		1.50	6.67

Appendix C, continued

Within-canopy negative xylem pressure potential													
Plant	DI	Habitat	Time of measure	1	2	3	4	5	6	7	8	mean	CV
3-12	3.229	bajada	predawn	3.0	3.2	4.0	4.0	3.8				3.60	13.03
3-16	3.326	bajada	predawn	4.1	4.2	5.4	4.5	5.0	4.4	4.0	4.2	4.48	10.87
3-24	4.975	bajada	predawn	2.3	2.6	2.8	2.6	2.1	2.7	2.6	2.2	2.49	10.18
3-11	1.039	road edge	midday	3.9	4.0	4.3	3.9	3.8	3.5	3.7	4.2	3.91	6.61
3-07	1.136	road edge	midday	5.0	4.2	5.1	3.9	3.9	4.9			4.50	12.49
3-18	1.569	road edge	midday	3.9	3.7	4.2	4.0	4.9	4.2			4.15	9.96
3-13	1.168	road edge	predawn	2.9	4.5	2.5	3.2	3.7	2.0	3.2		3.14	25.77